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RECURRENT APPEARANCE OF BISPORANGIATE STROBILI WITH PROLIFERATION ON *PICEA ABIES*

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ABSTRACT

Observations of mature Norway spruce, *Picea abies* (L.) Karst., that developed numerous bisporangiate strobili with proliferation were documented over a period of nine years. Most abnormal strobili had male characteristics at the proximal ends, female characteristics above, and vegetative proliferation at the distal ends. The degree of male, female, and vegetative characteristics varied among the hundreds of bisporangiate strobili observed, and there were many transitional stages. They appeared on one tree during eight spring-flushing seasons, on another during two seasons, and on five trees in the season following two environmental stresses: an insect infestation and a dry period which occurred when primordia were differentiating on developing embryonic shoots within buds.

Key Words: Norway spruce, *Picea abies,* bisporangiate strobili, vegetative proliferation, flowering, spruce mite, *Oligonychus ununguis,* environmental stress, Beltsville, Maryland

INTRODUCTION

Shoot apical meristems of *Picea* and other genera of Pinaceae normally differentiate and develop to produce strobili with exclusively male, female, or vegetative characteristics. Occasionally, embryonic shoots develop as mixtures of two or three of these morphological types. The results may be bisporangiate strobili (true hermaphrodites containing characteristics of both sexes), or reproductive structures with vegetative proliferation. In the latter case, rudimentary needles may be interspersed with bracts and ovuliferous scales, or they may emerge from distal ends of strobili as terminal proliferation.

The earliest documentation of bisporangiate strobili in conifers was made by Dickson (1860). Since then, there have been many published reports of bisporangiate strobili, with and without proliferation, in different species. Few reports were of observations within the genus *Picea* (Chamberlain, 1935; Pauley, 1942; Santamour, 1959; Elliott, 1979), and all were of a single occasion. Some authors conducted detailed anatomical examinations (Tosh and Powell, 1986), and others reported on dissections of one or a few specimens (Bartlett, 1913; Kirkwood, 1916; Holmes, 1932; Looney and Duffield, 1958). This report documents the recurrent development of bisporangiate strobili with vegetative prolifera-

Table 1. Summary of the abundance of reproductive strobili on all Norway spruce trees on the site, and of bisporangiate strobili with proliferation on specific trees. (Specific trees are denoted by letters corresponding to the order of appearance of bisporangiate strobili. Abundance scale: 1 = very rare, 2 = rare, 3 = infrequent, 4 = abundant, 5 = very abundant.)

	Abundance of Strobili on *Picea abies*			
	Reproductive Strobili on Trees on Site		Bisporangiate Strobili on Specific Trees	
Year of Observations	Male	Female	Tree	
1974	2	2	A	4
1975	4	2	A	3
1976	3	3	A	4
1977	2	1	A	2
			B	1
1978	5	3	A	4
1979	5	4	A	4
			B–E	3
1980	0	0	A	0
1981	4	2	A	2
1982	4	2	A	2

tion on mature trees of Norway spruce (*Picea abies* (L.) Karst.) observed during a period of nine years.

METHODS

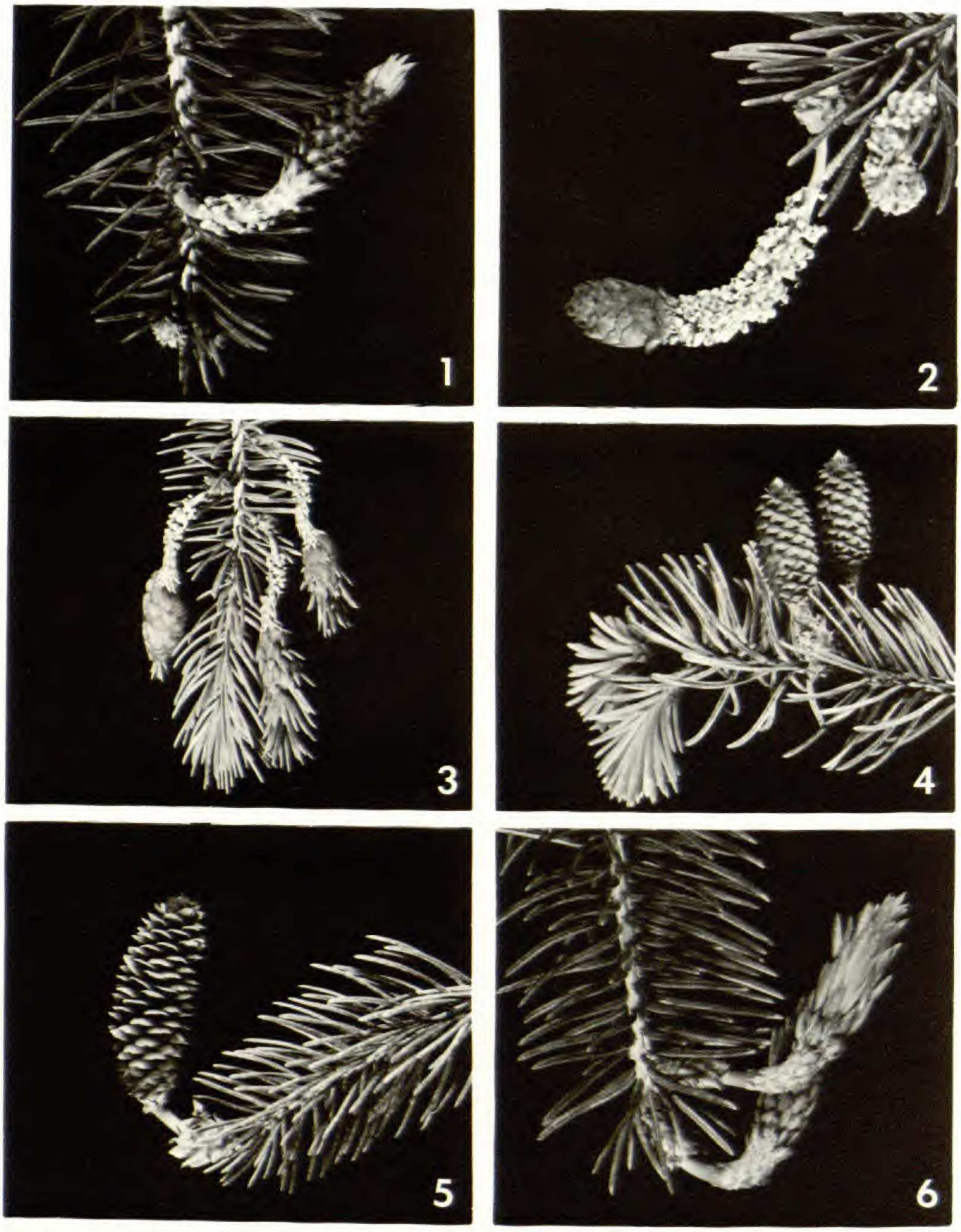
Annual observations were made on 27 mature, ornamental, Norway spruce trees that were planted in the 1930's at the Beltsville Agricultural Research Center, Beltsville, MD. The site had a gradually-sloping grade and well-drained soil. These and other trees in the locality had been observed and used as a source of embryonic shoots for anatomical and experimental studies since the early 1960's (Romberger, 1966; Varnell and Romberger, 1967; Romberger et al., 1970). The initial observations of bisporangiate strobili were made in May 1974, and continued each year thereafter, through June 1982. They were conducted at intervals throughout each spring-flushing period, under different daylight conditions, and with the aid of a telephoto lens. Some specimens were collected for photographing and closer examination, but most were left on the trees for continued observations. The abundance of reproductive strobili and bisporangiate strobili with proliferation were ranked on a numerical scale (Table 1).

Weather data collected for 27 years (1955 to 1982) at Beltsville Station No. 5 (located 1.6 km SSW of the site) were used to calculate the monthly means of the daily minimum, maximum, and average temperatures for each of the 9 years during which the trees were observed. In addition, long-term (27-year) monthly means of those parameters were calculated. Similarly, monthly precipitation values were summarized and long-term monthly means calculated. The 99% confidence interval for each monthly mean was determined by using the Student's t-distribution, and compared with individual monthly precipitation values from 1973 to 1982. Each month was classified as dry, normal, or wet, respectively, when the precipitation values were below, within, or above the confidence limits.

OBSERVATIONS

The proximal ends of bisporangiate strobili were male, and had slender peduncles attached to pre-existing shoots. Distinct, bright yellow microsporophylls at different developmental stages were often present (Figures 1–3), and some microsporangia released pollen. Pollen grains from several strobili were tapped onto an agar nutrient medium, and their viability was confirmed by the germination and elongation of pollen tubes. Many strobili had rudimentary female structures with intensely purple ovuliferous scales in the mid-sections, and vegetative proliferation that consisted of distinct, small, green and yellow tufts of needles protruding from the distal ends (Figures 1 and 4). Some strobili were without a vegetative segment (Figures 2 and 5). Others had a variety of the anatomical gradients including mixed transitional features of both female and vegetative structures. Many variants of these patterns were observed, but even when female (Figure 5) or vegetative (Figure 6) structures were dominant, the attachments were by male-like peduncles. Consequently, few bisporangiate strobili remained attached to the trees for more than a few months. Only one predominately female bisporangiate strobilus was observed that developed coriaceous, brown, cone scales, but they were smaller than normal and were sterile.

In 1974, more than 100 bisporangiate strobili, many exhibiting proliferation, were observed on Tree A. This was a vegetative year for other trees on the site, and both male and female (microsporangiate and megasporangiate) strobili were ranked as rare



Figures 1–6. Examples of the diversity among bisporangiate strobili and vegetative proliferation observed. Prominent features are referenced in the text. **1.** From Tree A, 1974. .91×. **2.** From Tree D, 1979. .72×. **3.** From Tree A, 1976. .58×. **4.** From Tree C, 1979. .67×. **5.** From Tree B, 1979. .64×. **6.** From Tree A, 1974. 1.02×.

(Table 1). In 1977, bisporangiate strobili appeared on Trees A and B. During July 1978, all the trees were heavily damaged by the spruce mite (*Oligonychus ununguis*) and displayed classic symptoms of bleached and bronzed flecking and stippling on the needles (Johnson and Lyon, 1976). September and October of that year were dry. During the subsequent growing season (1979), bisporangiate strobili with proliferation were observed on Trees A through E. In the summer of 1979, Kelthane (di(*p*-chlorophenyl)trichloromethylcarbinol) was applied to control another infestation of the spruce mite, and there was abundant precipitation during the summer and fall. During the following spring (1980), embryonic shoots were exclusively vegetative both on these trees and on trees located at nearby sites which were neither infested by the spruce mite nor sprayed with Kelthane.

DISCUSSION

In Maryland, bud initiation in *Picea* begins in late April, during the period of elongation of the newly emerging shoot. By midsummer, newly initiated primordia accumulate and differentiate into distinctively vegetative, male, or female organs that constitute the embryonic shoots (Romberger, 1966; Owens and Molder, 1977; Harrison and Owens, 1983). During this period, the developing embryonic shoots are susceptible to influences that may direct and alter the course of differentiation in primordia. Environmental stress has been cited as a probable cause of bisporangiate strobili by Santamour (1959), who observed such structures on several species of *Picea* during the spring following a severe drought year. Elliott (1979) documented the appearance of bisporangiate strobili on *Picea mariana* in a forest-tundra ecotone, and hypothesized that development of these structures was caused by stress in the arboreally marginal environment.

Attempts were made to determine if the observations reported here were correlated with weather data, but no consistent trends were detected. In some years, however, there appeared to be a correlation between the amount of precipitation during the months of embryonic shoot development and the subsequent emergence of reproductive structures. This correlation was especially true for a period of abundant precipitation during the summer and fall of 1979, which was followed by the absence of reproductive strobili, including bisporangiate strobili, in the spring of 1980 (Table 1). In two other instances, reproductive strobili were abundant (1978 and 1979, Table 1) following dry months in the summer and fall. These dry periods coincided with the time of primordia differentiation on the developing embryonic shoots. In addition, the spruce mite infestation during July 1978 imposed another environmental stress on the trees. This infestation, combined with the subsequent dry period, may have disrupted normal developmental sequences and resulted in the differentiation of various types of primordia on the embryonic shoots, as revealed when bisporangiate strobili with vegetative proliferation emerged from buds on five trees during the subsequent spring growth flush.

The recurrent development of bisporangiate strobili on one tree, and the fact that another tree of the same age and on the same site was predominately male during the years of observation, may reflect a genetic propensity for changes to occur in different degrees or at different rates among individuals. The differences may reflect phases of anatomical and sexual gradients that are characteristic within trees as they age (Prat, 1951). In that scheme, young trees have juvenile and sterile shoots, progress through male and female phases that include the appearance of hermaphroditic shoots, and culminate as old trees that may become purely male. Developmental changes expressed as anatomical gradients of sexual structures are probably associated with biochemical control mechanisms, such as altered concentration gradients of growth regulators, that may permit an established developmental sequence to change. These physiological gradients may be altered by stress in space over time.

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